

What is driving range expansion in a common bat? Hints from thermoregulation and habitat selection



Leonardo Ancillotto^a, Ivana Budinski^b, Valentina Nardone^a, Ivy Di Salvo^a, Martina Della Corte^c, Luciano Bosso^a, Paola Conti^d, Danilo Russo^{a,e,*}

^a Wildlife Research Unit, Dipartimento di Agraria, Università degli Studi di Napoli Federico II, Via Università 100, 80055 Portici, NA, Italy

^b Department of Genetic research, Institute for biological research "Siniša Stanković", University of Belgrade, Bulevar despota Stefana 142, 11060 Belgrade, Serbia

^c Dipartimento di Biologia, Università degli Studi di Napoli Federico II, Complesso Universitario Monte S. Angelo, 80126 Napoli, Italy

^d Ente Parco Nazionale del Vesuvio, Palazzo Mediceo, Via Palazzo del Principe, 80044 Ottaviano, NA, Italy

^e School of Biological Sciences, University of Bristol, 24 Tyndall Avenue, BS8 1TQ, Bristol, UK

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ABSTRACT

Human-induced alterations of ecosystems and environmental conditions often lead to changes in the geographical range of plants and animals. While modelling exercises may contribute to understanding such dynamics at large spatial scales, they rarely offer insights into the mechanisms that prompt the process at a local scale. Savi's pipistrelle (*Hypsugo savii*) is a vespertilionid bat widespread throughout the Mediterranean region. The species' recent range expansion towards northeastern Europe is thought to be induced by urbanization, yet no study actually tested this hypothesis, and climate change is a potential alternative driver. In this radio-telemetry study, set in the Vesuvius National Park (Campania region, Southern Italy) we provide insights into the species' thermal physiology and foraging ecology and investigate their relationships with potential large-scale responses to climate, and land use changes. Specifically, we test whether *H. savii* i) exploits urbanisation by selecting urban areas for roosting and foraging, and ii) tolerates heatwaves (a proxy for thermophily) through a plastic use of thermoregulation. Tolerance to heatwaves would be consistent with the observation that the species' geographic range is not shifting but expanding northwards. Tracked bats roosted mainly in buildings but avoided urban habitats while foraging, actively selecting non-intensive farmland and natural wooded areas. *Hypsugo H. savii* showed tolerance to heat, reaching the highest body temperature ever recorded for a free-ranging bat (46.5 °C), and performing long periods of overheating. We conclude that *H. savii* is not a strictly synurbic species because it exploits urban areas mainly for roosting, and avoids them for foraging; this questions the role of synurbation as a range expansion driver. On the other hand, the species' extreme heat tolerance and plastic thermoregulatory behaviour represent winning traits to cope with heatwaves typical of climate change-related weather fluctuations.

1. Introduction

Understanding changes in the geographical distribution of organisms in the Anthropocene is a complex task because synergic or contrasting human pressures may influence them, and modifications may become conspicuous only over large spatial scales and extended periods (Sánchez-Mercado et al., 2010). Effects of anthropogenic pressures may be relevant at both local (e.g. reduction of occurrence area following land use change) and global (e.g. climate change) scales. Climate and land use changes are two of the major drivers of biotic homogenization worldwide, inducing large-scale rearrangements of species assemblages

(Jetz et al., 2007). Range expansions, shifts or contractions often reflect a species' ability to cope with such changes (Maiorano et al., 2011; Rebelo et al., 2010), and mostly depend on its ecological niche breadth and phenotypic or niche plasticity. While thermal physiology may play a pivotal role to survive to (or even thrive in) new climatic conditions (Huey et al., 2012), the way organisms exploit habitat – whether they do it selectively or opportunistically – may determine their chances of success in confronting habitat loss, alteration or fragmentation. Such characteristics may translate into different patterns of distributional changes: understanding the functional traits that influence thermal tolerance and habitat use flexibility has therefore paramount

* Corresponding author at: Wildlife Research Unit, Laboratorio di Ecologia Applicata, Dipartimento di Agraria, Università degli Studi di Napoli Federico II, Via Università 100, 80055 Portici, NA, Italy.

E-mail address: danrusso@unina.it (D. Russo).

importance in explaining range shifts and disentangling the ecological factors underlying them. Spatial modelling may help tackle such processes on large geographical scales (e.g. Bosso et al., 2016; Kirkpatrick et al., 2017), but it often lacks the high resolution needed to bring to light the mechanistic processes that operate locally (Russo and Ancillotto, 2015). Individual-based, empirical approaches are therefore those that often perform best in unveiling the small-scale processes from which large-scale patterns emerge (Huey et al., 2012).

Urbanization is one of the dominant causes of today's land use change: it affects species' reproductive success, demography, and distribution in very different ways, depending on how efficiently organisms exploit the novel resources and conditions encountered in human settlements and infrastructures (Lowry et al., 2013). For species flexible enough to become synurbic (Francis and Chadwick, 2012), urbanization may open new avenues to range expansion through continuous or discontinuous (stepping-stone) pathways (Davis and Glick, 1978). Tolerance to increasing temperatures, or temperature extremes associated with heatwaves, may on the other hand permit persistence where temperatures have significantly risen (Parmesan, 2006).

While synurbic habits are easy to record, detecting individual physiological efficiency in coping with climate change is more challenging. Environmental temperatures influence a range of physiological processes, such as maintenance of water balance, thermoregulation, and resistance to overheating (Huey et al., 2012). The latter property increases survival prospects during heatwaves, yet its energetic costs may decrease individual fitness by affecting reproduction or foraging efficiency (Speakman and Król, 2010).

Bats are excellent taxa for testing hypotheses on the effects of human-driven environmental modifications on animals. Most species are multi-habitat specialists, i.e. they require diverse habitat features at different spatial scales and times of their life cycles for roosting or foraging, which makes them sensitive to land use changes (Jones et al., 2009). Bats from temperate areas use daytime torpor and hibernation and require distinct roost microclimatic conditions depending on whether they are overwintering or reproducing. Therefore, they are responsive to ambient temperatures and their alterations at different scales (Geiser, 1998). Sex also plays a major role in the way bats exhibit such requirements: in summer, males largely use daytime torpor to save energy and reduce water loss (Bondarenco et al., 2016; Speakman et al., 2003), while females do it less to avoid slowing down embryo development or depressing milk production (McAllan and Geiser, 2014). Finally, bats show a high body surface area to volume ratio caused by their small size and a large extension of wing membranes, so they are also indirectly sensitive to high temperatures since these may increase evaporative water loss (Korine et al., 2016). Strong, sudden dehydration due to heatwaves is probably one the greatest constraints posed by climate change to bats and may lead to mass mortality (Flaquer et al., 2014; O'Shea et al., 2016; Welbergen et al., 2008). Tolerance to temperature peaks (implying resistance to dehydration) is, therefore, a chief factor in influencing the fate of bat populations under warming climate scenarios (Adams and Hayes, 2008; Korine et al., 2016). Overheating, i.e. the increase in body temperature above the thermo-neutral zone, is a strategy adopted by some endotherms, including bats, to reduce the steepness of thermal gradient between body and ambient temperatures and thus decrease conductive and convective heat gains (Maloney et al., 1999; Marom et al., 2006). This comes at a cost, however, because increasing metabolic rates associated with high body temperatures requires extra energy (Bartholomew et al., 1970). Bats may, therefore, enter torpor following an overheating phase to recover the amount of energy (and water) lost in the process (Bondarenco et al., 2016, 2014; Maloney et al., 1999).

The geographic range of some common European bat species has expanded over the last decades (e.g. Ancillotto et al., 2016; Lundy et al., 2010; Uhrin et al., 2016). For Kuhl's pipistrelle *Pipistrellus kuhlii*, whose European range has recently increased more than fourfold, distribution modelling identified climate change as the most important driver, but

failed to explain whether urbanization also plays a role at a finer spatial scale (which is likely to be the case, because the species is largely synurbic) due to the insufficient resolution of that approach (Ancillotto et al., 2016). Another species showing a recent, remarkable range expansion is Savi's pipistrelle *Hypsugo savii* (Uhrin et al., 2016). Its main distribution encompasses Southern Europe and Northern Africa through the Middle East and the Caucasus to Central Asia and Northern India (Mickleburgh et al., 2002). Since the 1990s, the species has reached Central and Eastern Europe: although urbanization may have influenced the process (Uhrin et al., 2016), there is no clear evidence supporting this hypothesis, and climate change is another candidate driver (Rebelo et al., 2010), perhaps in synergy with urbanization. This ecologically flexible bat species spans across a broad altitudinal range and uses an array of habitats (Ancillotto et al., 2017, 2014; Di Salvo et al., 2009; Uhrin et al., 2016). No investigation, however, has yet examined the species' thermoregulatory behaviour or habitat selection. In this radio-telemetry study, we provide an insight into the species' thermal physiology and foraging ecology to test two competing, non-mutually exclusive hypotheses on the species' range expansion:

- 1) *Synurbization hypothesis.* *H. savii* is a synurbic specialist that forages (or roosts) preferentially in urban habitats, so we hypothesize that its range expansion may have been due to urbanization and predict that the species will select urban habitats for both roosting and foraging;
- 2) *Thermal tolerance hypothesis.* *H. savii* tolerates temperature peaks associated with heatwaves, which represents a proxy for thermophily, and may overcome thermal barriers posed by climate change persisting or even thriving in the areas of its original distribution that are warming. This hypothesis is consistent with the observation that the geographic range is not shifting but expanding, northwards. Thermophily would also allow *H. savii* to colonize new areas characterized by a warmer climate. We, therefore, predict that *H. savii* will tolerate high ambient temperatures through overheating.

2. Materials and methods

2.1. Study area

We set our study in the Vesuvius National Park, a protected area covering ca 8500 ha within the municipality of Naples (Lat: 40°49'N, Long: 14°25'E) comprising Mount Vesuvius, and its surrounding territory. The landscape comprises a mosaic of natural habitats, including both coniferous and broadleaved forests (25%), Mediterranean scrubland and lava-rocky areas (15%) generated by past volcanic events. Human-modified habitats are common, accounting for more than half of the overall park territory, and comprise residential urban areas (30%), non-intensive farmland, and orchards (30%).

2.2. Capture and tagging

In June-July 2016 we mistnetted *H. savii* at an artificial pond. We measured forearm length and body mass of captured individuals to the nearest 0.1 mm and 0.1 g, respectively; age, sex, and reproductive conditions were assessed following Racey (1988). To measure daytime skin temperature patterns and record spatial behaviour, we fitted bats with temperature-sensitive radio-transmitters (LB-2XT, Holohil Systems, Ontario, Canada; Table 1). Tag's weight never exceeded 5% of the bat's body mass.

2.3. Roosting behaviour and foraging habitat selection

We detected tag radio-signals with a Sika telemetry receiver (Biotrack Ltd, UK) connected to a three-element Yagi antenna. The location error, estimated following Zimmermann and Powell (1995), was $\pm 8.7^\circ$ (SD). Bats were tracked continuously around-the-clock

Table 1

Date of capture, sex, reproductive status, biometry (BM = body mass, FAL = forearm length), colony size, and tracking details of 12 *Hypsugo savii* radiotracked at the Vesuvius National Park in Southern Italy. Nr = non reproductive; Lac = lactating; Pr = pregnant; n/a = not assessed.

Bat Code	Date of capture	Sex	Status	BM (g)	FAL (mm)	Colony size	N foraging fixes	Max. distance from roost (km)	Home Range area (km ²)
209752	27/06/2016	M	Nr	5.6	32.8	1	31	0.3	0.2
209754	27/06/2016	M	Nr	5.9	32.0	n/a	33	3.8	3.5
209756	27/06/2016	M	Nr	5.8	33.0	3	35	3.1	3.8
209757	20/06/2016	M	Nr	6.1	33.0	n/a	33	3.4	2.4
209758	27/06/2016	M	Nr	5.6	32.0	1	38	5.5	1.6
209759	20/06/2016	M	Nr	5.6	33.5	2	43	3.3	4.1
Mean ± SD (males)				5.8 ± 0.2	33.1 ± 0.4	1.8 ± 1.0	35.5 ± 4.4	3.7 ± 0.9	2.6 ± 1.5
209761	02/07/2016	F	Lac	7.1	36.7	7	49	0.4	0.7
209763	02/07/2016	F	Lac	7.5	34.3	5	33	4.6	1.0
209771	02/07/2016	F	Lac	8.7	36.7	7*	31	3.7	0.75
209772	20/06/2016	F	Nr	6.1	34.0	3	33	1.3	3.1
209751	20/06/2016	F	Pr	7.8	32.8	n/a	32	3.2	1.4
209753	20/06/2016	F	Pr	8.0	35.6	6	33	2.8	1.2
Mean ± SD (females)				7.5 ± 0.9	35.0 ± 1.6	5.6 ± 1.7	35.2 ± 6.8	2.67 ± 1.6	1.4 ± 0.9
Mean ± SD (total)				6.7 ± 1.1	33.9 ± 1.7	3.9 ± 2.4	35.3 ± 5.5	2.9 ± 1.6	2.0 ± 1.4

* + 25 individuals of *Pipistrellus kuhlii*.

(White and Garrott, 1990). In the daytime, we found bat roosts following signal direction and once we identified a roost, we established the exit location by observing bats taking off at emergence time when we also assessed colony size. In the night, once we detected a bat, we took several bearings in rapid sequence. The bat was either located by ‘homing in’ on the subject (e.g. Entwistle et al., 1996; Russo et al., 2002), i.e. approached on foot as close as possible, or through triangulation from different bearing locations. Rapid, directional movements between distant sites were interpreted as commuting; when a bat stayed active over a restricted area, its behaviour was classified as foraging (Russo et al., 2002). For each fix, the operator position was recorded with a “Dakota10” Garmin GPS receiver (Garmin, USA, 5–15 m accuracy) and the direction of the signal taken with a compass. We obtained a high contact time (on average > 95%) for all individuals and recorded fixes every 10 min to minimize autocorrelation (Ancillotto et al., 2015a,b; Hillen et al., 2009).

We performed spatial analysis with ArcGIS 9.2 (ESRI). We used Hawth’s Analysis Tools rel. 3.27 to generate Minimum Convex Polygons (MCP) that encompassed the fixes of each bat to obtain individual home ranges, and an MCP comprising all bat fixes to delimit ex-post the study area boundaries. We assigned habitat types to all foraging fixes employing the 2012 IV-level Corine Land Cover (available from <http://www.sinanet.isprambiente.it/it/sia-ispra/download-mais/corine-land-cover/>) and referring to its classification. We ground-validated the above assignment through field surveys. We identified six habitat types, as follows:

- Rocky areas (rocky surfaces and cliffs);
- Mediterranean scrubland, dominated by *Cytisus scoparius*, *Genista aetnensis*, and *Spartium junceum* with few or no trees;
- Mixed coniferous forest, comprising artificial conifer (*Pinus pinea*, *Pinus pinaster*, *Pinus nigra*) plantations, associated with broadleaved trees (*Quercus ilex*, *Robinia pseudoacacia*);
- Broadleaved forest, mainly comprising *Quercus ilex* and *Robinia pseudoacacia*;
- non-intensive farmland, comprising small, traditionally-managed fields, orchards, and vineyards;
- Urban-discontinuous areas, i.e. residential areas interspersed with gardens and public green areas.

We assessed habitat selection by compositional analysis (Aebischer et al., 1993), using R’s “adehabitatSH” package (Calenge, 2013). To test this, we used two approaches (Aebischer et al., 1993). In a “second order analysis”, the available habitat was established as the amount of the different habitats falling within an MCP that encompassed all fixes

of each individual; and habitat use was expressed as the habitat composition recorded within individual home ranges. We also performed a “third order analysis”, where habitat use was represented by the number of fixes recorded in each habitat type, while habitat availability was that recorded within individual home ranges. We explored inter-sexual differences in colony size, home range sizes and maximum distances travelled from roost to foraging sites by tagged bats using Wilcoxon signed-rank tests.

2.4. Thermal profiling

Pulse emission rate of temperature-sensitive tags changes according to the tagged bat’s skin temperature (T_s), which can, therefore, be inferred using unit-specific calibration curves provided by the manufacturer. We checked the reliability of calibration in the laboratory for a subset of tags, following Stawski and Geiser (2012).

In daytime (taken as the daylight time interval between a bat’s return to the roost and its evening emergence), we measured the time during which the tag emitted 21 pulses, for three consecutive time intervals 15 min apart. At the same time, we also measured ambient temperature (T_a) with a digital thermometer ($\pm 0.1^\circ\text{C}$) placed in the shade near the roost at a height of 1.5 m above ground. Roost structure and location precluded any measurement of roost’s internal temperatures, so we used external temperature: although this was probably lower than internal temperature, it made it possible to carry out consistent comparisons over space and time.

Roost type and individual reproductive status can influence bat thermoregulatory behaviour (Grinevitch et al., 1995; Solick and Barclay, 2006), so in thermoregulation analysis, we only included bats roosting in buildings (i.e. the most commonly used roost type) and controlled for reproductive status by including only non-reproductive males and reproducing females. From each bat we measured: daily maximum ($T_{s\text{-max}}$) and minimum ($T_{s\text{-min}}$) skin temperatures; active temperature ($T_{s\text{-act}}$; i.e. temperature assessed 15 min before a bat left the roost; (Dietz and Kalko, 2006; Nardone et al., 2015)); temperature of torpor onset T_{onset} established as in Willis and Brigham (2007); this latter value represents a standardized threshold differentiating body temperatures of torpid individuals from body temperatures of normothermic individuals in small mammals (Willis, 2007).

Contrary to torpor, little is known about the physiology of overheating in bats (Bondarenco et al., 2016, 2014; Maloney et al., 1999; Marom et al., 2006); due to a lack of a univocal definition in the scientific literature, we assumed bats to be overheating when $T_s > T_{s\text{-act}}$.

We measured the above temperatures to obtain the following daily thermal behaviour descriptors: use of torpor (i.e. whether a bat was

recorded with $T_s < T_{\text{onset}}$); torpor maximum depth (equalling $T_{\text{onset}} - T_s$ min); torpor duration (i.e. time in minutes a bat spent at $T_s < T_{\text{onset}}$); overheating intensity (equalling $T_{\text{s-max}} - T_{\text{s-act}}$) and time spent in overheating (i.e. time, expressed in min, that a bat spent at $T_s > T_{\text{act}}$).

We also explored the effect of mean ambient temperature on overheating duration and intensity with a linear regression. We tested whether the above descriptors differed between males and females by running Generalized Linear Mixed Models (GLMMs) using sex as a fixed factor and individual identity as a random effect. In all models, we adopted a backward stepwise variable selection according to AICc values, from a first full model also including mean daily temperature as a covariate, resulting in a final model that only included variables having significant ($p < 0.05$) effects (Minimum Adequate Models); this model selection was performed with the function stepAIC available in the MASS package (Ripley et al., 2013).

3. Results

We followed 12 adult bats (six males and six females), corresponding, on average, to three consecutive radiotracking days and nights per bat, and three complete sessions of daily T_s measurements. For each bat, we obtained 31–49 (10–17 per night/bat) foraging fixes (Table 1).

3.1. Synurbization hypothesis: roosting behaviour and foraging habitat selection

We established the exact location of 14 roosts; tagged bats never shared roosts, and only two bats (both males) used more than one roost. All roosts except one (a rock crevice used by a solitary male) were in buildings – cracks in walls or spaces beneath tiles. Colonies numbered 3–7 bats, but one reproductive female roosted along with 6 conspecifics and 25 *P. kuhlii*. The tagged females roosted in larger groups than did the males (range: 3–7 vs 1–3 individuals, respectively; $W = 1.2$, $p < 0.01$). Bats emerged from roosts 16.0 ± 13.0 min (mean \pm SD) after sunset, showing no significant intersexual difference ($W = 0.45$, n.s.).

Home ranges measured, on average $2.0 \pm 1.3 \text{ km}^2$ (Fig. 1; Table 2), and the mean straight distance bats covered between roosts and foraging sites was $2.9 \pm 1.6 \text{ km}$. Males had home ranges almost twice those of females ($W = 25.0$, $p < 0.01$) and moved longer straight distances between roosts and foraging sites than females ($W = 26.1$,

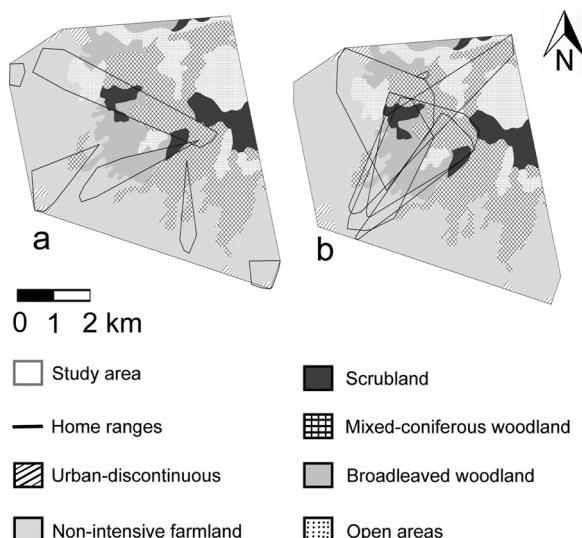


Fig. 1. Home ranges of 12 Savi's pipistrelles *Hypsugo savii* radiotracked in the Vesuvius National Park, Southern Italy, expressed as 100% Minimum Convex Polygons; a) females ($n = 6$), b) males ($n = 6$).

$p < 0.05$).

When compared to the study area's habitat availability, habitat use was non-random ($\lambda = 0.35$, $p < 0.05$), and preferences ranked as follows ($>$ indicate a significant difference between habitat types): Non-intensive farmland $>$ Mixed-coniferous woodland $>$ Broadleaved woodland $>$ Urban-discontinuous $>$ Scrubland $>$ Rocky areas. When habitat availability was assessed within individual home ranges, again habitat use was non-random ($\lambda = 0.48$, $p < 0.01$) and ranked as follows: Non-intensive farmland $>$ Scrubland $>$ Mixed-coniferous woodland $>$ Broadleaved woodland $>$ Urban-discontinuous $>$ Rocky areas. In both analyses, urban habitats had a minor importance for foraging compared to farmland and most natural habitats within individual home ranges, rejecting the synurbization hypothesis (Table 2).

3.2. Thermal tolerance hypothesis: thermal profiling

In agreement with the thermal tolerance hypothesis, bats showed hyperthermia. The diurnal ambient temperature during the study period ranged between 23.1°C and 30.9°C ; tagged bats showed marked T_s oscillations during the day, with a minimum value of 23.1°C (equalling, in that case, T_a) and peaks up to 46.5°C . All tagged individuals performed long bouts of overheating every day ($472.0 \pm 207.4 \text{ min/day}$); the intensity of overheating ranged between 1.6°C and 11.6°C and averaged $6.5 \pm 3.3^\circ\text{C}$.

All tracked bats performed at least one torpor bout during the study period (90% and 20% of tracking days for males and females, respectively), spending on average $176.4 \pm 147.2 \text{ min/day}$ in torpor.

Thermoregulatory behaviour differed between males and females (Fig. 2): in the latter, body temperature oscillations were narrower (i.e. higher minimum and lower maximum temperatures; both $p < 0.05$), use of torpor less frequent ($p < 0.001$), torpor bouts shorter and shallower (both $p < 0.001$), and overheating phases less intense and shorter (both $p < 0.05$; Table 3) than in males. Ambient temperature negatively influenced torpor depth ($\beta = -0.52$; $p < 0.05$), i.e. bats exhibited shallower torpor bouts on warmer days.

4. Discussion

We offer a first insight into the physiology and spatial ecology of *H. savii*, providing evidence of the species' extensive thermal tolerance and selective habitat use, on which bases we argue that a warming climate, rather than urbanization may be fostering the range expansion recorded for this species (Uhrin et al., 2016). Since we only tracked a limited number of individuals in one study region, our findings warrant confirmation from the analysis of larger samples and other geographic areas.

All but one bat we tracked roosted in buildings, and all preferred foraging in non-intensive farmland and forest over urban areas. However, in other regions, such as Croatia, *H. savii* often roosts in natural roosts, i.e. crevices in limestone pavements (Kipson et al., 2014). Roosting in urban areas may be a way for this thermophilous species to exploit the higher temperatures associated with the heat-island effect (Arnfield, 2003). *H. savii* might, therefore, be an urban-tolerant species rather than an urban exploiter (Kark et al., 2007; Russo and Ancillotto, 2015).

Sex also affected spatial behaviour: females had smaller home ranges and travelled shorter distances than did males. Intersexual differences in ecological and behavioural traits are common among bats, including differences in habitat selection (Ibáñez et al., 2009; Mata et al., 2016; Russo, 2002; Senior et al., 2005), movement (Kerth et al., 2002), thermoregulation (Grinevitch et al., 1995; Russo et al., 2017), and reactions to habitat alteration (Rocha et al., 2017). Although due to sample size limitations we could not compare the spatial behaviour exhibited by females across different reproductive conditions, the only non-reproductive female we tracked had the largest home-range. Moreover, lactating females travelled shorter distances from the roost

Table 2

Home range size and percent habitat composition of 12 *Hypsugo savii* radiotracked at the Vesuvius National Park in Southern Italy. Available habitat was quantified as that comprised within a minimum convex polygon encompassing all bat fixes.

Bat Code	Home range size (km ²)	Rocky areas (%)	Broadleaved woodland (%)	Mixed-coniferous woodland (%)	Scrubland (%)	Non-intensive farmland (%)	Urban-discontinuous (%)
209751	1.42	0.0	29.6	0.0	17.6	52.8	0.0
209752	0.2	0.0	10.0	90.0	0.0	0.0	0.0
209753	1.2	0.0	53.3	7.5	10.0	29.2	0.0
209754	3.52	6.5	42.0	17.3	7.1	27.0	0.0
209756	3.79	11.4	29.6	32.2	12.0	14.8	0.3
209757	2.38	0.4	31.5	8.4	5.0	54.6	0.0
209758	1.58	1.3	0.6	53.2	28.5	16.5	0.0
209759	4.1	5.6	54.4	14.9	17.1	8.0	0.0
209761	0.66	0.0	0.0	0.0	0.0	100.0	0.0
209763	1.01	0.0	0.0	0.0	0.0	97.0	3.0
209771	0.75	0.0	0.0	16.0	0.0	84.0	0.0
209772	3.14	20.4	10.2	38.5	11.5	19.4	0.0
Mean ± SD	2.0 ± 1.4	3.8 ± 6.4	21.8 ± 20.9	23.2 ± 26.8	9.1 ± 8.9	41.9 ± 35.1	0.3 ± 0.9
Study area	41.71	12.90	7.29	22.70	13.83	40.49	2.78

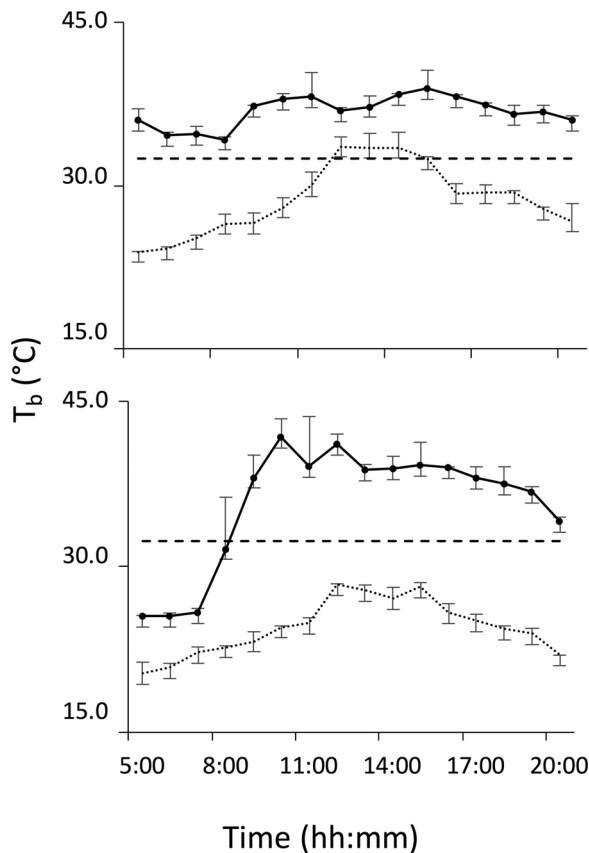


Fig. 2. Thermal profiles of one male (above) and one female (below) Savi's pipistrelles *Hypsugo savii*, radiotracked in the Vesuvius National Park, Southern Italy. Solid line: bat's body temperature; dotted line: ambient temperature; dashed line: torpor threshold. In the time axis label, hh = hours, mm = minutes.

to their foraging areas than did pregnant and non-reproductive females, confirming that reproductive status may alter spatial behaviour (Henry et al., 2002; Encarnação et al., 2004), and thus influence individual responses to habitat alteration. We also found that tagged females stayed in groups that were larger than those where males were found, and in one case they shared the roost with *P. kuhlii* (Ancillotto et al., 2013). The difference in group size between tagged males and females is similar to what known for other species, where males are often solitary or live in small aggregations (e.g. Russo et al., 2017).

Our results also indicate that *H. savii* may tolerate temperature extremes such as heatwaves through prolonged overheating phases at high temperatures, reaching the highest body temperature ever recorded in a free-ranging bat (46.5 °C), and ranking above *Mormopterus* sp. (45.8 °C, Bondarenco et al., 2014). Overheating is an effective strategy adopted by endotherms to reduce the temperature gradient between the body surface and the outer environment, decreasing heat gain and associated cell damage (Maloney et al., 1999; Marom et al., 2006). This physiological response, however, implies increased metabolic rates and water loss (Speakman and Król, 2010). The lack of relationship between ambient temperature and overheating duration or intensity in our study may be due to microclimatic conditions inside the roost. Spaces beneath roof tiles may accumulate heat and expose bats to overheating: roosts in buildings and other artificial structures are in fact typically warmer than rock crevices (Lausen and Barclay, 2002), and can reach very high temperatures (Maloney et al., 1999) that might prove lethal to sensitive bat species (Flaquer et al., 2014; Welbergen et al., 2008). Although all bats we tracked performed both torpor and overheating, females showed narrower body temperature oscillations, which might render them more sensitive to heatwaves than males and perhaps reduce the species' ability to exploit increasing temperatures under a climate change scenario, e.g. by limiting reproductive success after intense heat events (see Amorim et al., 2015).

Overall, our results and those of previous studies (e.g. Di Salvo et al., 2009; Kipson et al., 2014) show that *H. savii* uses roosts opportunistically but tend to forage away from urban areas, while as a thermophilous species may sustain increased ambient temperatures. Under different climate change scenarios, *H. savii* is predicted to expand its geographic range up to over 220% according to modelling work (Rebelo et al., 2010). While increasing temperatures at higher latitudes are probably allowing this species to expand its range northwards, thermal tolerance will be crucial to let *H. savii* persist in its original areas of occurrence from where the new environmental conditions might displace other, more sensitive, species. We argue that thermophily, rather than synurbization, is playing a central role in influencing *H. savii* range expansion. A number of bat species are experiencing range expansions probably due to climate change: *Nyctalus noctula* (Godlevska, 2015), *Pipistrellus nathusii* (Lundy et al., 2010), *Pipistrellus kuhlii* (Ancillotto et al., 2016; Sachanowicz et al., 2006), and *Tadarida brasiliensis* (McCracken et al., 2018). Although *P. kuhlii*'s fourfold range expansion across Europe is explained as a response to increasing temperature, urbanization also likely plays a role at a local scale. In fact, this species improves reproductive success by roosting in urban matrices (Ancillotto et al., 2015a,b) where suitable foraging habitat such as artificially lit sites can be found (Maxinová et al., 2016; Tomassini et al., 2014). We remark, however, that while some bat species may

Table 3

Effects of sex and ambient temperature on the daily thermoregulatory behaviour of 11 adult Savi's pipistrelle, *Hypsugo savii* (6 males and 5 females) tracked in the Vesuvius National Park (southern Italy) during June-July 2016, assessed with generalized linear mixed models.

Response	R ²	Model	Estimate ± SE	t	p
Use of torpor	0.20	Sex	0.429 ± 0.159	2.693	< 0.001
Min. skin temperature	0.63	Sex	-5.362 ± 0.820	-6.539	< 0.001
Max. skin temperature	0.12	Sex	2.094 ± 0.998	2.099	< 0.05
Time spent in torpor	0.52	Sex	195.189 ± 43.146	-4.524	< 0.001
Torpor depth	0.69	Sex	3.409 ± 0.876	3.887	< 0.001
		Mean ambient temperature	-0.522 ± 0.215	-2.434	< 0.05
Overheating intensity	0.46	Sex	4.502 ± 0.949	4.747	< 0.001
Time spent in overheating	0.12	Sex	145.48 ± 68.81	2.870	< 0.05

perform better than many others under climate change, an increasing frequency and severity of heatwaves, normally associated to droughts, may still affect negatively even the bat species that are adapted to increasing temperatures through a reduction in water or food availability. Our results not only indicate *H. savii* as a novel potential exploiter of climate change but also highlight the importance of investigating individual-based responses, such as changes in spatial behaviour and physiology, for understanding both local and large-scale modifications of species' geographical ranges.

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